Title: Effects of vegetation on soil microbial C, N, and P dynamics in a tropical forest and savanna of central Africa

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Abstract

The forest–savanna transition zone is widely distributed on nutrient-poor Oxisols in central Africa. To reveal and compare the nutrient cycle in relation to soil microbes for forest and savanna vegetation in this area, we evaluated seasonal fluctuations in microbial biomass carbon (MBC), nitrogen (MBN), and phosphorus (MBP) for 13 months as well as soil moisture, temperature, soil pH levels, and nutrients for both vegetation types in eastern Cameroon. Soil pH was significantly lower in forest (4.3) than in savanna (5.6), and soil N availability was greater in forest (87.1 mg N kg⁻¹ soil) than in savanna (32.9 mg N kg⁻¹ soil). We found a significant positive correlation between soil moisture and MBP in forest, indicating the importance of organic P mineralization for MBP, whereas in savanna, we found a significant positive correlation between soil N availability and MBP, indicating N limitation for MBP. These results suggest that for soil microbes, forest is an N-saturated and P-limited ecosystem, whereas savanna is an N-limited ecosystem. Additionally, we observed a significantly lower MBN and larger MB C:N ratio in forest (50.7 mg N kg⁻¹ soil and 8.6, respectively) than in savanna (60.0 mg N kg⁻¹ soil and 6.5, respectively) during the experimental period, despite the rich soil N condition in forest. This may be due to the significantly lower soil pH in forest, which influences the different soil microbial communities (fungi-to-bacteria ratio) in forest versus savanna, and therefore, our results indicate that, in terms of microbial N dynamics, soil pH rather than soil substrate conditions controls the soil microbial communities in this area. Further studies should be focused on soil microbial community, such as PLFA, which was not evaluated in the present study.

Key words

Soil microbial dynamics; Seasonal fluctuations; Soil pH; Central Africa; Vegetation

1. Introduction

Central Africa contains the second largest area of contiguous moist tropical forest in the world, covering approximately 2 million km² (Mayaux et al., 2005; Duveiller et al., 2008). Forest conservation and reforestation in this area is a global environmental issue because tropical forest (and indeed all forest) ecosystems act as carbon sinks (Laporte et al., 2007; Lewis et al., 2009) and also maintain high and specific biodiversity levels (Brooks et al., 2001; Martin et al., 2013). In the Guineo-Congolese region, which includes the northern extreme of the African tropical forest, forests are surrounded by periforest savannas that constitute a forest–savanna transition zone (Sankaran et al., 2005; Duveiller et al., 2008). The impact of slash-and-burn agriculture and logging in this area will increase in the future, resulting in serious deforestation and increasing areas of savanna vegetation. Once the mature forest is cleared, reforestation is very difficult because of the strongly weathered nutrient-poor soil (Oxisols), which is widely distributed in this region (Yemefack et al., 2005; Nguetnkam and Dultz, 2011). To implement forest preservation or reforestation of savanna, it is necessary to understand the soil nutrient dynamics of each vegetation type.

Generally, when comparing nutrient dynamics between the tropical forest and savanna, forest is limited by soil P supply, whereas savanna is limited by soil N supply (Vitousek and Farrington, 1997; Vitousek et al., 2010). Our previous studies comparing the soil C, N, P, and other mineral stocks between forest and savanna in eastern Cameroon also revealed that forests have higher soil N stock, indicating N-rich ecosystems, possibly due to N-fixing tree dominance, whereas savannas have lower soil N stock, indicating N-poor ecosystems (Sugihara et al., 2014). In addition, soil P availability is lower in forest than in savanna, indicating the P-limited status of forest ecosystems in eastern Cameroon (Sugihara et al., 2014). On the basis of the soil nutrient stock information, we considered that forests are N-rich and possibly P-limited ecosystems, whereas savannas are N-limited ecosystem in the central African forest–savanna

transition zone. However, these information were mainly originated from nutrient stock studies but not from nutrient dynamics studies (Cleveland et al., 2002). To understand the characteristics of biogeochemical cycles in the African tropical forest and savanna, it is necessary to understand the detailed soil N and P dynamics with special reference to nutrient relocation.

Soil microbes play an important role in the biogeochemical cycle as “decomposers” and “nutrient sink-sources” (Singh et al., 1989; Wardle 1992; Wardle et al., 2004), and they are very sensitive to environmental conditions, such as quality and quantity of the soil substrate (Wang et al., 2003; Liu et al., 2006), temperature and moisture conditions (Fang and Moncrief, 2001; Hamel et al., 2006), and soil chemical conditions (Moreno et al., 1999; Baath and Anderson, 2003). As a result, many researchers have used soil microbial characteristics as indicators of soil fertility in various ecosystems or various land use. (Joergensen and Emmerling, 2006; Bastida et al., 2008), as well as for indexing the limiting nutrient or environmental factors in ecosystems (Cleveland and Liptzin, 2007; Gnakambary et al., 2008). Because the size of microbial biomass (MB) is mainly controlled by the amount of substrate, MB carbon (MBC) has been used as a good indicator of soil fertility (Joergensen and Emmerling, 2006). Using the MB C:N, C:P, and N:P ratios, it is possible to predict the nutrient that limits the soil microbial dynamics, which indicates the nutrient limiting the ecosystem (Galicia and Garcia-Oliva, 2004; Aponte et al., 2010). Chen et al. (2003) compared the seasonal fluctuation of MBC and MB phosphorus (MBP) for forest and grassland in New Zealand and found a faster MBP turnover rate in forest than in savanna, indicating the importance of MBP as a P pool in P-limited forest ecosystems. Therefore, we compared the nutrient flow for forest and savanna in this area by measuring the soil microbial dynamics.

Soil microbes, however, are quite sensitive to soil moisture and temperature conditions, which result in distinct seasonal fluctuations in a year, even under the same land management

(Wardle, 1992, 1998; Bardgett et al., 2007). Thus, it is necessary to evaluate the soil microbial dynamics for an entire year. Moreover, seasonal fluctuations of soil microbes play important roles as temporal nutrient sink-sources for plant nutrient uptake, especially in the dry tropics (Singh et al., 1989; Wardle, 1992). Many studies have found that soil moisture primarily affects the soil microbial dynamics; soil MB is high in the dry season, and thus retains nutrients when plant activity is low. In contrast, during the rainy season, soil MB is low because of accelerated turnover caused by enhanced grazing by soil macro-fauna and because of microbial cell lysis due to drastic changes in soil moisture. The nutrient release from soil microbes during the rainy season contributes to plant uptake as a nutrient source. In eastern Cameroon, there are clear dry and rainy seasons during a year, although the annual rainfall is relatively high (ca. 1500 mm year⁻¹) compared with the rainfall reported in studies that investigated the seasonal dynamics of soil microbes in the tropics (ca. 600–1200 mm year⁻¹) (Chen et al., 2005; Hamel et al., 2006; Sugihara et al., 2010). Because there is little information about the seasonal fluctuations of soil microbes in tropical forest and savanna in central Africa, it is necessary to evaluate whether soil microbes fluctuate seasonally in these ecosystems and their relation to nutrient dynamics.

Therefore, our objectives were (1) to evaluate the seasonal fluctuations of soil microbial C, N, and P levels over a year, (2) to evaluate the effects of vegetation on the soil microbial dynamics, and (3) to reveal the biogeochemical cycle of adjacent tropical forest and savanna in central Africa.

2. Material and methods

2.1. Description of study sites

We conducted the field experiment from the beginning of July 2011 to the end of July 2012 (13 months) at two sites with different vegetation types, forest (FOR) and savanna (SAV),

in an eastern province of Cameroon, which is in the forest–savanna transition zone (Mertens and Lambin, 2000; Guillet et al., 2001). This area is located in the northern part of the Southern Cameroon Plateau, which is the dominant geographical feature of Cameroon, and Oxisols are generally distributed (Soil Survey Staff, 2006; Sugihara et al., 2014). The elevation is ca. 650–700 m. Our field measurements from 2008 to 2012 indicated that the mean annual temperature was ca. 23.5°C and the annual rainfall was ca. 1350–1550 mm. In this area, the rainy season is usually bimodal, with two rainy seasons: the long rainy season (from September to November) and the short rainy season (from March to July). The FOR site is an old forest site, which had grown for more than 50 years since the last slash-and-burn cultivation, and the SAV site is a typical savanna type in this area, which is mainly dominated by *Chromolaena odorata* (Koutika et al., 2004; Koutika and Rainey, 2010). Our vegetation survey showed that the dominant forest vegetation was *Albizia zygia*, which abounded in the tree layer. *Myrianthus arboreus* was also an abundant tree species (Sugihara et al., 2014). In both vegetation, soil surface was mostly covered by each plant biomass. Our interviews with local people indicated that the SAV site had been continuously maintained with its present vegetation for more than 10 years, although wild and/or artificial fire had occurred (once every 1–4 years). The sites are located within 7 km of one another; thus, the weather, including rainfall, conditions and soil materials were the same over the study period (Sugihara et al., 2014). Table 1 presents detailed site descriptions and soil characteristics of the surface layer (0–10 cm). Soil C:N ratio in FOR was substantially lower (11.8) compared with SAV (16.2) because of the dominance of N-fixing trees in the FOR site, and this was the general condition in this area according to our former study (Sugihara et al., 2014). Both soils were classified as Typic Kandiodox (Soil Survey Staff, 2006).

2.2. Soil environmental monitoring

At the FOR and SAV sites, the soil moisture content (10-cm depth) and air and soil temperatures (5-cm depth) were measured. The monitoring was performed hourly in two replicates using a data logger system (CS616 probes for soil moisture and 107 thermistor probes for temperature were connected to a CR-1000 data logger; Campbell Scientific, Inc.). Rainfall was monitored hourly at nearby villages (ca. 3 km from each site), using the same CR1000 data logger system and a TE525MM device (Campbell Scientific, Inc.).

2.3. Soil sampling and analyses

Soil samples were collected nine times, 11 July, 22 July, 21 Sep, and 20 Nov 2011, and 28 Jan, 8 Feb, 20 Mar, 8 May, and 13 July 2012, at FOR and SAV during the experimental period, which completely covered both of the dry and rainy seasons. At each site, we first determined the sampling area for the vegetation survey as 50 × 50 m, and then, chose three representative sub-plots (10 × 10 m). For each soil sample, five surface soil samples (0–10 cm) were taken inside the sub-plot (10 × 10 m; avoiding the plot edge), and the five soil samples were combined and mixed as one soil composite sample for each sub-plot (three replications). Soil samples were immediately transported to the lab in a 4°C cooler, sieved through a 4-mm mesh screen after removing visible plant debris, and stored under field-moist conditions at 4°C until analysis. Samples were taken to determine the gravimetric moisture content (GMC) of soil, MBC, MBP, and MB nitrogen (MBN), as well as extractable C (Ext-C), N (Ext-N), and P (Ext-P). After sieving, 10 g of each soil sample was weighed in a glass vial and placed in a 105°C oven for 48 h, and the dry weight was recorded. GMC was the difference in soil weight before and after oven drying. MBC and MBN were measured in duplicate for each soil sample using the fumigation–extraction method (Brookes et al., 1985; Vance et al., 1987). Briefly, soil samples (8 g dry base) were fumigated with ethanol-free chloroform for 24 h at 25°C. After

removal of the chloroform, soluble C and N were extracted from fumigated and non-fumigated samples in 32 ml of 0.5 M K₂SO₄ for 30 min on an orbital shaker. Total organic C and extractable N in the filtered extract were determined using a TOC-N Auto-analyzer (TOC-V carbon analyzer with an IN unit, Shimadzu). Microbial C flush (the difference in extractable C from fumigated and non-fumigated samples) was converted to MBC using a factor of 0.45 (Vance et al., 1987). Microbial N flush was converted to MBN using a factor of 0.54 (Brookes et al., 1985). In the current study, the K₂SO₄-extractable C and N from non-fumigated soil samples were used as a measure of Ext-C and Ext-N, respectively (Beck et al., 1997; Hamel et al., 2006). MBP was determined in triplicate by simultaneous liquid fumigation and extraction using anion-exchange resin membranes in bicarbonate form for 48 h as described by Kouno et al. (1995); however, hexanol was used as the fumigant instead of chloroform (McLaughlin and Alston, 1986; Butterly et al., 2009). Briefly, soil samples (2 g dry base) were shaken and extracted in a 40-ml mixture of deionized water and resin for 18 h. For fumigated samples only, 1 ml of hexanol was added. The resin was then removed and rinsed in deionized water, and the phosphate was recovered by shaking for 1 h in 20 ml of 0.5 M HCl. Extracted P was measured colorimetrically using the molybdate-ascorbic acid procedure (Murphy and Riley, 1962), after adjusting the pH, with p-nitrophenol as the indicator. Absorbance was determined at 712 nm. Because our soil samples are Oxisols, which have a high P-fixation capacity, some of the released inorganic P in solution can be fixed by the soils during the extraction process (Oberson et al., 1997). Subsamples containing inorganic P spiked to equal 0, 2.5, 5.0, or 10.0 mg P kg⁻¹ were also determined to account for the sorption of P released during the extraction period (Khan and Joergensen, 2012). According to this pre-analysis, 89.7% of released P (n = 5) was recovered and used for correction. Microbial P flush was converted to MBP using a factor of 0.40 (Brookes et al., 1982). In the current study, the resin-extractable P from non-fumigated soil samples was used as a measure of Ext-P (Butterly et al., 2009).

2.4. Statistical analyses

All statistical analyses were performed with SYSTAT v.11 (SYSTAT Software, Richmond, CA, USA). All data are expressed on a dry-weight basis. The effects of vegetation and sampling time (seasonal variation) were assessed using a repeated-measures analysis of variance (ANOVA). Pearson's correlation coefficient was also used to estimate overall correlations between the MB measured and the environmental and substrate variables at both sites. All variables were tested for normality of the distribution before the analysis. In all cases, $P < 0.05$ was considered significant.

3. Results

3.1. Seasonal variations of soil environments

The total rainfall during the experimental period (13 months) was 1728 mm, and most rain fell (ca. 80% of total rainfall) in the rainy seasons from August to November 2011 and from April to June 2012 (Fig. 1). In the experimental year, sporadic rainfall during the dry season was unusually high, especially in February 2012, resulting in a relatively wet dry season, which caused relatively high soil moisture content. According to the hourly soil moisture measurements recorded by the data logger, the volumetric moisture content (VMC: 10 cm) in FOR and SAV tended to be high in the rainy season and low in the dry season (Fig. 1). Numerous dry-wet cycles were observed only in SAV, even in the rainy seasons from September to December 2011 and from February to July 2012, although they were not observed in FOR. This is because the well-developed forest canopy suppressed the water evaporation in FOR, but not in SAV. As a result, VMC fluctuations were relatively large in SAV compared with FOR during the experimental period. In addition, the GMC of soil samples (0–10 cm) in the FOR fluctuated from 18.2 to 24.3% (coefficient of variation (CV) 9.0%), and the GMC in SAV

fluctuated from 12.9 to 24.0% (CV 24.1%), indicating our soil sampling covered the various moisture conditions. According to repeated-measures ANOVA, the GMC of soil samples were also significantly lower in SAV than in FOR during the experimental period (Table 2).

The average daily air temperature during the experimental period was 22.8°C, and the average daily soil temperatures at 5 cm were 22.5°C and 24.4°C in the FOR and SAV, respectively. The soil temperature in FOR was generally lower compared with in SAV (Fig. 1).

The soil pH in FOR ranged from 4.0 to 4.5 (CV 3.6%) and from 5.1 to 6.0 in SAV (CV 4.9%) (Fig. 2). Soil pH was lower in FOR than in SAV throughout the experimental period (Table 2). In general, the soil pH should be lower in forest ecosystems compared with savanna ecosystems in similar soil and climate conditions because of the strong acidification caused by forest growth (Alfredsson et al., 1998; Dezzio et al., 2004).

3.2. Seasonal variations in soil microbial biomass and nutrients

In FOR, MBC varied from 342.7 to 536.8 mg C kg⁻¹ soil (CV 13.9%), MBN varied from 39.3 to 63.5 mg N kg⁻¹ soil (CV 16.4%), and MBP varied from 24.8 to 45.6 mg P kg⁻¹ soil (CV 17.5%) during the experimental period (Fig. 3). In SAV, MBC varied from 335.2 to 414.4 mg C kg⁻¹ soil (CV 7.0%), MBN varied from 43.6 to 76.1 mg N kg⁻¹ soil (CV 17.0%), and MBP varied from 26.9 to 41.6 mg P kg⁻¹ soil (CV 12.9%) (Fig. 3). MBC and MBN fluctuated during the experimental period in both FOR and SAV, but MBP did not fluctuate in either FOR or SAV (Table 2). According to repeated-measures ANOVA, the MBC in FOR was greater than in SAV, whereas MBN in FOR was less than in SAV (Table 2). There was no significant difference in MBP between FOR and SAV (Table 2).

MB C:N, C:P, and N:P ratios in FOR fluctuated from 6.7 to 11.0 (CV 17.3%), from 8.4 to 17.5 (CV 23.4%), and from 1.1 to 1.8 (CV 16.0%), respectively (Fig. 4). In SAV, MB C:N, C:P, and N:P ratios fluctuated from 5.1 to 8.6 (CV 18.0%), from 9.3 to 14.4 (CV 14.8%), and

from 1.2 to 2.6 (CV 24.1%), respectively (Fig. 4). All ratios in FOR and SAV fluctuated substantially during the experimental period. This was especially true for the MB C:N and C:P ratios in FOR, which clearly increased in the dry period, as sampled on 28 Jan and 20 Mar 2012, but not in SAV. The MB C:N ratio was significantly higher in FOR than that in SAV, whereas the MB N:P ratio was significantly lower in FOR than that in SAV (Table 2). The MB C:P ratios in FOR and SAV were not significantly different ($P < 0.05$) (Table 2).

In FOR, Ext-C varied from 277.2 to 356.6 mg C kg⁻¹ soil (CV 7.7%), Ext-N varied from 60.2 to 117.3 mg N kg⁻¹ soil (CV 26.1%), and Ext-P varied from 1.3 to 7.0 mg P kg⁻¹ soil (CV 73.3%) (Fig. 3). In SAV, Ext-C varied from 133.3 to 187.3 mg C kg⁻¹ soil (CV 13.3%), Ext-N varied from 23.9 to 43.1 mg N kg⁻¹ soil (CV 21.1%), and Ext-P varied from 2.0 to 4.1 mg P kg⁻¹ soil (CV 23.0%) (Fig. 3). All values fluctuated significantly throughout the experimental period in both sites, but more seasonal fluctuation was observed in FOR than in SAV. Ext-C and Ext-N values were significantly higher in FOR than in SAV, whereas the Ext-P value was lower in FOR than in SAV (Table 2).

Ext-C:N, Ext-C:P, and Ext-N:P ratios in FOR fluctuated from 2.6 to 5.6 (CV 27.6%), from 44.5 to 272.7 (CV 40.1%), and from 16.8 to 61.0 (CV 29.4%), respectively. In SAV, Ext-C:N, Ext-C:P, and Ext-N:P ratios fluctuated from 3.6 to 7.7 (CV 28.2%), from 34.8 to 86.9 (CV 30.1%) and from 9.0 to 17.6 (CV 23.4%), respectively. All values fluctuated significantly throughout the experimental period. The Ext-C:N ratio was significantly lower in FOR than in SAV, whereas the Ext-C:P and Ext-N:P ratios were clearly larger in FOR than in SAV (Table 2).

3.3. Relationship between soil microbial values and soil environment

Table 3 shows the result of a Pearson's correlation analysis between the soil microbial values and soil environmental conditions, such as soil moisture, air and soil temperatures, substrates, and soil pH. In FOR, soil moisture positively correlated with MBP and negatively

correlated with the MB C:P ratio ($P < 0.05$). Ext-N also negatively correlated with MBN ($P < 0.05$). In addition, we observed a weak negative correlation between soil moisture and the MB C:N ratio ($r = -0.64$, $P = 0.06$), and weak positive correlations between air temperature and MBC ($r = 0.56$, $P = 0.12$), between soil pH and MBN ($r = 0.64$, $P = 0.06$), and between soil temperature and MBP ($r = 0.58$, $P = 0.10$).

On the other hand, in SAV, only Ext-N significantly correlated with soil MB values ($P < 0.05$), including a positive correlation with MBP and a negative correlation with the MB C:P ratio. Moreover, we observed a weak negative correlation between soil moisture and MB C:N ratio ($r = -0.57$, $P = 0.11$), and a weak positive correlation between soil temperature and MBP ($r = 0.55$, $P = 0.13$).

4. Discussion

4.1. Effect of vegetation on soil microbial dynamics

In the present study, we found that the maintained MBC was larger in FOR than in SAV. Because the Ext-C, which is a substrate for soil microbes, was consistently greater in FOR than in SAV (Fig. 3), it contributes to the larger MBC in FOR (Zaman et al., 1999). However, MBN was smaller in FOR than in SAV, even though the Ext-N was substantially larger in FOR than in SAV. As a result, the MB C:N ratio was significantly higher in FOR than in SAV, indicating a lower microbial N content in FOR than in SAV. This result is quite interesting because of its apparent contradiction: a low MBN level and high MB C:N ratio in FOR, which has rich N in soil. This could be explained by the existence of different microbial communities that survive in soils of different chemical compositions in FOR and SAV. Many studies have found that fungi dominate in forest ecosystems and bacteria dominate in savanna ecosystems because of different soil pH levels (Aciego and Brookes, 2008; Rousk et al., 2010). Generally, fungi is higher MB C:N ratio than bacteria (Anderson and Domsch, 1980); therefore, fungi are

the dominant species in FOR, where the MB C:N ratio is high, whereas bacteria are the dominant species in SAV, where the MB C:N ratio is low. Baath and Anderson (2003) found that soil pH affects soil microbial communities and concluded that the fungi-to-bacteria ratio increases as the soil pH decreases. In the current study, we found a significantly lower soil pH level in FOR than in SAV (Table 2) and that a positive correlation between the soil pH level and MBN occurred only in FOR (Table 3), indicating that there is a soil pH-limited MBN value in FOR. However, the substrate quality should also be considered, although we did not evaluate it in the current study (Bossuyt et al., 2001; Six et al., 2006). Lauber et al. (2008) found that in the southeastern US, the fungi-to-bacteria ratio was higher in forest than in grassland soil because of the different substrate qualities, such as the high C:N content of forest and low C:N content of grassland. Our results indicated that soil pH (and possibly litter quality) could be the primary factors affecting the soil microbial compositions, such as fungi-to-bacteria ratio, and MBN dynamics between the different vegetation types, rather than the amount of available N substrate, such as Ext-N (Rousk et al., 2010). Because we did not evaluate the soil microbial community or the litter quality of both vegetation types, further studies are necessary to evaluate the effects of soil pH and litter quality on the soil microbial community.

MBP dynamics in FOR and SAV were similar and, unlike MBC and MBN, did not fluctuate significantly throughout the experimental period (Table 2). It indicates that soil microbes play an important role as a stable P nutrient pool in both vegetation of Oxisols (Oberson et al., 2001). Kaspari et al. (2008) revealed that the tropical rain forest uptake is 6.4 kg P ha⁻¹ annually in Panama, and it was estimated at 6.6 kg P ha⁻¹ annually in the present FOR (unpublished data). Tondoh et al. (2013) also reported that *Chromolaena odorata*, which is the same plant species in SAV, uptakes 3.6 kg P ha⁻¹ annually in Ivory Coast, and it was estimated at 2.1 kg P ha⁻¹ annually in the present SAV (unpublished data). Ext-P (2.3 and 4.0 kg P ha⁻¹ at 0–10 cm in FOR and SAV, respectively) is similar to, or rather less than, the annual P uptake in

each vegetation type, whereas MBP (35.4 and 47.4 kg P ha⁻¹ at 0–10 cm in FOR and SAV, respectively) is larger than the annual P uptake in each vegetation type. This indicates the significance of soil microbes as a stable nutrient pool for plant P uptake in this region. Interestingly, there are different limiting factors for MBP between FOR and SAV (Table 3). Because we observed a positive correlation between Ext-N and MBP only in SAV, the amount of N substrate must limit MBP in SAV, indicating N limits for soil P dynamics. However, only soil moisture positively correlated with MBP in FOR, possibly indicating (1) no substrate limitations for MBP and (2) the importance of soil organic matter (SOM) decomposition for MBP in FOR. Because Ext-P in FOR did not correlate with MBP (Table 3), it appears that the amount of P substrate did not limit the MBP variations in FOR. However, the amount of Ext-P (1.3–7.0 mg P kg⁻¹ soil) seems to be too small to explain the MBP variations (24.7–45.6 mg P kg⁻¹ soil). This suggests that the current analytical method of determining Ext-P (the Resin method) is not sufficient to evaluate the MBP dynamics, at least in this region and/or soil. Khan and Joergensen (2012) found that NaHCO₃-extractable organic P was closely related to MBP, based on laboratory analyses using various soil samples. Because of soil moisture, which controls the SOM decomposition rate and was positively correlated with MBP in FOR, the decomposed organic P should be an important P source for soil microbes in FOR, indicating a P substrate limitation in FOR. Our present results suggest that, in terms of soil microbial dynamics, forests are N-saturated, P-limited ecosystems, and savannas are N-limited ecosystems in this region.

4.2. Factors controlling seasonal variations in soil microbes in each vegetation type

In the present study, there was no clear difference in MBC, MBN, and MBP values between the rainy and dry seasons in FOR and SAV (Fig. 3), although we found a positive relationship between soil moisture and MBP in FOR. This indicates that soil microbes in this

region do not act as a temporal nutrient sink-source with seasonal changes, which was observed in another dry tropical climate region (Singh et al., 1989). This may have resulted from the larger annual rainfall and the exceptionally weak dry season in the current experimental period, which was caused by exceptional rainfall in the dry season. Past research, which reported the distinct seasonal fluctuations of soil microbes, has been generally conducted in dry climate regions, having rainfall of ca. 600–1200 mm year⁻¹ and more than 2–4 completely dry months in a year (Wardle, 1992; Chen et al., 2005; Sugihara et al., 2010).

However, we found a distinct temporal fluctuation of soil microbes during the experimental period. The most drastic fluctuation of soil microbes in FOR was observed on 8 Feb 2011 during the dry season, following an unusually large rainfall (36.5 mm on ~6–7 Feb 2011). MBC in FOR clearly decreased from 28 Jan 2011 to 8 Feb 2011, with increasing soil moisture. The rapid decrease in MBC may have been caused by an osmotic shock to the soil microbes during the dry–wet event that resulted from the substantial and immediate increase of soil moisture by rainfall in the dry season (Halverson et al., 2000; Fierer and Schimel, 2003). On the other hand, MBC in SAV did not decrease on 8 Feb 2011 and did not clearly fluctuate compared with FOR, indicating that the soil microbes in SAV must be well adapted to the dry–wet cycles of soil (Kieft et al., 1987; Fierer and Schimel, 2002). Because severe dry–wet cycles of soil are normal for SAV but not for FOR (Fig. 1), the soil microbes in SAV experience numerous dry–wet cycles, resulting in a stable amount of MBC on 8 Feb 2011. However, this is not the case for FOR, where soil microbes could not adapt to the dry–wet cycle, resulting in osmotic shock. Fierer and Schimel (2002) found that soil microbes could adapt after experiencing several dry–wet cycles under laboratory conditions. Therefore, our results indicate that soil microbes in FOR respond differently to the dry–wet cycles during the dry season than those in SAV, because of the different histories of soil moisture fluctuations. On the other hand, MBP in FOR and MBN in SAV increased on 8 Feb 2011 after the unusual rainfall, with an

increase of Ext-P in FOR and Ext-N in SAV. These results indicate that the SOM decomposition should be important to the increase of MBP in FOR and MBN in SAV during the dry season. As we have already discussed above, because FOR in this region is an N-saturated, and possibly P-limited, ecosystem, only MBP increased in FOR; however, because SAV is an N-limited ecosystem, only MBN increased in SAV. In addition, because we also found a positive correlation between Ext-N and MBP in SAV during the experimental period (Table 3), Ext-N must also be a controlling factor, not only for MBN but also for MBP, in SAV in this region.

5. Conclusion

We found a larger soil N availability and lower soil pH in FOR compared with in SAV, and we found positive relationships between soil moisture and MBP in FOR, and between Ext-N and MBP in SAV, indicating a P-limited FOR ecosystem and an N-limited SAV ecosystem. In addition, contrary to the rich soil N substrate conditions in FOR, we found a lower MBN value and higher MB C:N ratio in FOR than in SAV. This indicates that substrate conditions should not be the primary controlling factor of MBN dynamics in this area. Other soil environmental values indicate that soil pH is the primary controlling factor affecting the microbial communities (fungi:bacteria ratio) in each vegetation type. Further studies are necessary to assess the effects of soil pH and other factors, such as litter quality, on soil microbial communities in forest and savanna in this region.

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Table 1. Description of the study sites and soil physicochemical characteristics of surface layer (0–10 cm) soil in the forest and savanna vegetation of eastern Cameroon.

Site	Latitude Longitude	Altitude	pH (1:5 water)	Soil texture (%)			Total C	Total N	Total P
				Sand	Silt	Clay	(g kg ⁻¹)		(mg kg ⁻¹)
Forest	N 04°35' E 13°15'	700 m	4.3	39.9	4.9	55.2	18.8	1.6	448.9
Savanna	N 04°32' E 13°15'	677 m	5.6	38.7	8.0	53.3	29.1	1.8	450.5

Table 2. Summary of average values, and results of repeated-measures ANOVA for the effects of vegetation and seasonal fluctuation on each value (N = 9 for averages, and N = 54 for repeated-measures ANOVA).

	MBC	MBN (mg kg ⁻¹ soil)	MBP	MB C:N ratio	MB C:P ratio	MB N:P ratio	Soil pH (1:5 water)
Forest	425.5	50.7	37.3	8.6	11.9	1.4	4.3
Savanna	379.2	60.0	35.4	6.5	11.0	1.7	5.6
Vegetation (V)	F = 12.7 P = 0.02	F = 27.3 P = 0.006	NS	F = 557.2 P < 0.001	NS	F = 29.3 P = 0.006	F = 801.4 P < 0.001
Seasonal Variation (S)	F = 3.0 P = 0.01	F = 8.0 P < 0.001	NS	F = 19.6 P < 0.001	F = 3.8 P = 0.003	F = 5.9 P < 0.001	F = 5.9 P < 0.001
S*V	NS ^a	F = 2.9 P = 0.02	NS	F = 4.1 P = 0.002	F = 3.1 P = 0.01	NS	NS
	Ext-C	Ext-N (mg kg ⁻¹ soil)	Ext-P	Ext- C:N ratio	Ext- C:P ratio	Ext- N:P ratio	GMC ^b (%)
Forest	314.6	87.1	2.4	3.9	166.5	42.7	21.5
Savanna	163.1	32.9	3.0	5.3	58.5	11.4	18.9
Vegetation (V)	F = 187.2 P < 0.001	F = 264.5 P < 0.001	F = 36.4 P = 0.004	F = 15.2 P = 0.02	F = 252.7 P < 0.001	F = 336.4 P < 0.001	F = 30.9 P < 0.01
Seasonal Variation (S)	F = 5.7 P < 0.001	F = 12.7 P < 0.001	F = 29.3 P < 0.001	F = 18.6 P < 0.001	F = 32.0 P < 0.001	F = 12.4 P < 0.001	F = 48.3 P < 0.001
S*V	NS	F = 4.2 P = 0.002	F = 33.3 P < 0.001	F = 3.2 P = 0.01	F = 29.8 P < 0.001	F = 19.6 P < 0.001	F = 5.0 P < 0.001

a: NS means not significant.

b: GMC means gravimetric moisture contents of soil.

Table 3. Correlation coefficient between soil microbial factors and the environmental and soil nutrient factors for each vegetation during the experimental period (July 2011 to July 2012) in eastern Cameroon (N = 9 for each vegetation).

Forest	MBC	MBN	MBP	MB C:N ratio	MB C:P ratio	MB N:P ratio
Soil moisture	NS ^a	NS	0.68*	-0.64 [#]	-0.74*	NS
Air Temperature	0.56 [#]	NS	NS	NS	NS	NS
Soil Temperature	NS	NS	0.58 [#]	NS	NS	NS
Ext-C	NS	NS	NS	NS	NS	NS
Ext-N	NS	-0.67*	NS	NS	NS	NS
Ext-P	NS	NS	NS	NS	NS	NS
soil pH	NS	0.64 [#]	NS	NS	NS	NS
Savanna	MBC	MBN	MBP	MB C:N ratio	MB C:P ratio	MB N:P ratio
Soil moisture	NS	NS	NS	-0.57 [#]	NS	NS
Air Temperature	NS	NS	NS	NS	NS	NS
Soil Temperature	NS	NS	0.55 [#]	NS	NS	NS
Ext-C	NS	NS	NS	NS	NS	NS
Ext-N	NS	NS	0.75*	NS	-0.78*	NS
Ext-P	NS	NS	NS	NS	NS	NS
soil pH	NS	NS	NS	NS	NS	NS

* indicates $P < 0.05$

indicates $P < 0.15$

a: NS means not significant.

Figure 1. Fluctuation of rainfall and volumetric moisture content (VMC) (0–10 cm) (a), and air and soil temperature (5 cm) in forest and savanna during the experimental period (July 2011 to July 2012) in eastern Cameroon.

VMC data from July to mid September 2011 in forest could not be obtained because of technical problems with the sensors.

Figure 2. Seasonal fluctuation of soil pH in the forest and savanna during the experimental period (July 2011 to July 2012) in eastern Cameroon. Bars indicates the standard error (N = 3).

Figure 3. Seasonal fluctuation of soil microbial biomass (MB) carbon (C) (a), nitrogen (N) (b), and phosphorus (P) (c), as well as extractable (Ext) C (a), N (b), and P (c) in the forest and savanna during the experimental period (July 2011 to July 2012) in eastern Cameroon. Bars indicates the standard error (N = 3).

Figure 4. Seasonal fluctuation of soil microbial biomass (MB) carbon:nitrogen (C:N) ratio (a), C:phosphorus (P) ratio (b), and N:P ratio (c) in the forest and savanna during the experimental period (July 2011 to July 2012) in eastern Cameroon. Bars indicates the standard error (N = 3).